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Homogenisation of carnivorous mammal ensembles caused by global range reductions of large-bodied hypercarnivores during the late Quaternary

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Abstract

Carnivorous mammals play crucial roles in ecosystems by influencing prey densities and behaviour, and recycling carrion. Yet, the influence of carnivores on global ecosystems has been affected by extinctions and range contractions throughout the Late Pleistocene and Holocene (~130 000 years ago to the current). Large-bodied mammals were particularly affected, but how dietary strategies influenced species' susceptibility to geographic range reductions remains unknown. We investigated 1) the importance of dietary strategies in explaining range reductions of carnivorous mammals (≥5% vertebrate meat consumption), and 2) differences in functional diversity of continental carnivore ensembles by comparing current, known ranges to current, expected ranges under a present-natural counterfactual scenario. The present-natural counterfactual estimates current mammal ranges had modern humans not expanded out of Africa during the Late Pleistocene and were not a main driver of extinctions and range contractions, alongside changing climates. Ranges of large-bodied hypercarnivorous mammals are currently smaller than expected, compared to smaller-bodied carnivorous mammals that consume less vertebrate meat. This resulted in consistent differences in continental functional diversity, whereby current ensembles of carnivorous mammals have undergone homogenisation through structural shifts towards smaller-bodied insectivorous and herbivorous species. The magnitude of ensemble structural shift varied among continents, with Australia experiencing the greatest difference. Weighting functional diversity by species' geographic range sizes caused a three-fold greater shift in ensemble centroids than when using presence-absence alone. Conservation efforts should acknowledge current reductions in the potential geographic ranges of large-bodied hypercarnivores and aim to restore functional roles in carnivore ensembles, where possible, across continents.

Keywords: *carnivores, global-change, macroecology, community disassembly, extinctions*

1. Introduction

In the coming century, anthropogenic extinctions are predicted to shift global mammal assemblages towards small-bodied insectivores [1]. Yet, mammal extinctions influenced by humans are not only a future, or recent, phenomenon but began during the Late Pleistocene (130 000 to 11 700 years ago) and continued throughout the Holocene (11 700 years ago to the current) [2–4], henceforth collectively referred to as the late Quaternary. During the Late Pleistocene, modern humans expanded out of Africa in waves [5] and colonised the inhabited continents, which, in combination with changing climates [6–8], caused globally widespread mammal range modifications and extinctions [9–12]. Mammal assemblages were further modified by direct human-induced range contractions of extant species during the Holocene [13,14]. Large-bodied mammals on continents were particularly susceptible to range reductions (extinctions and range declines, collectively) throughout the late Quaternary [15], which reduced ecological processes such as nutrient and seed dispersal [16,17]. However, knowledge is limited on whether certain dietary strategies influenced species' susceptibility to late Quaternary range reductions. Here, we address this knowledge gap for carnivorous mammals by investigating whether late Quaternary range reductions were biased towards hypercarnivorous species (those consuming ≥70% vertebrate meat [18,19]), and how continental ensembles of carnivorous mammals were modified since modern humans expanded out of Africa. We refer to continental ensembles as pools of species in specified geographic areas (i.e. continents) consuming a shared resource (vertebrate biomass) and are phylogenetically restricted (Mammalia) [20].

Diet is a crucial ecological trait, which interacts with body mass to influence behaviour [21] and ecological function [22]. Mammals with carnivorous diets consume animal biomass following hunting or scavenging [23]. Ecological effects of predatory carnivores include the potential to influence the behaviour and populations of their prey [24]. Indirectly, these interactions can influence vegetation consumption rates and patterns [25], and prevent mesopredator release [26]. Scavengers contribute to nutrient cycling by consuming carrion, which can stabilise food webs [23]. However, carnivore extinctions [27] and widespread range contractions of extant carnivores [13,28] have occurred in response to anthropogenic pressures, including habitat fragmentation [29,30], prey depletion [31,32], and direct persecution [33]. Such recent effects of modern humans on carnivorous mammals may mirror prehistorical ones, particularly, the reduction of prey diversity and abundance [32].

Diets are typically variable, and it is uncommon for species to be true dietary specialists with only 23.7% of mammals primarily consuming a single food type (e.g. vertebrate meat or fruit) [34]. However, hypercarnivores, like Felidae, are true specialists of vertebrate meat [18,19]. Throughout mammalian evolution large-bodied, hypercarnivorous clades have evolved and subsequently disappeared, likely unable to adapt to ecological disturbances because of intrinsic traits including specialised resource requirements and slow life-histories [35,36]. Dietary and behavioural specialism determine a species' ecological niche and influence its ability to respond to disturbances and fluctuation in resource availability [37,38]. In stable environments dietary specialists are thought to thrive while preferred resources are abundant, whereas generalists thrive in unpredictable environments with varied resource availability [39].

Disturbance events can create selection pressures that can be neutral or selective with respect to species' ecological traits [40,41], and can be represented by changes in the structure of multidimensional functional trait space [41]. Extinctions of large-bodied mammals, in response to modern human arrival [10,11,42,43] and changing climates [6–8], was a filtering process that led to functional diversity reduction in North American mammals [44], as well as for Carnivora above 10kg worldwide [27]. In Africa, carnivore functional groups have been largely retained [27]. Yet, previous estimates of continent-wide changes in late Quaternary functional diversity have considered extinctions without considering geographic range contractions of extant species [e.g. 33], and so functional diversity declines may be underestimated.

Here, we investigated whether current geographic ranges of hypercarnivorous mammals are more restricted than those of less carnivorous mammals, and consequently how functional diversity of continent-wide ensembles have been affected. We compared the current, known geographic ranges of mammals in response to widespread human presence and changing climates throughout the late Quaternary, to a present-natural counterfactual scenario [45]. The present-natural represents current, expected ranges of mammals had modern humans not expanded out of Africa and, alongside changing climates, contributed to late Quaternary range reductions. Comparing current and present-natural ranges provides insights into how prehistoric and historic effects of modern humans, alongside changing climates, influenced the current geographic ranges of carnivorous mammals (Fig. S1). We assessed if (i) mammals with more carnivorous diets have larger differences between current and present-natural ranges than mammals with less carnivorous diets, (ii) differences in continental functional diversity of carnivorous mammal ensembles between current and present-natural are consistent and

suggestive of trait filtering, and (iii) differences in functional diversity is underestimated when excluding the lost geographic ranges of extinct and extant species.

2. Methods

2.1. Species selection and functional traits

The Phylogenetic Atlas of Mammals database (Phylacine) was used for species selection [46]. Carnivorous mammals were selected as those reported to consume ≥ 5% vertebrate meat, and to be terrestrial (coded 1 in Phylacine) and not aerial, freshwater or marine (0). Humans (Genus: *Homo*) were excluded from our analyses. These criteria returned 1081 species from 15 orders, with 12% classed as hypercarnivorous (Fig. S2; those consuming ≥70% vertebrate meat [18,19]).

For each species, we extracted functional traits from Phylacine describing two key dimensions of a species' ecological niche: body mass (g), averaged across sex and geographical location (as previously defined [47]), and diet, expressed as the average percentage of food consumed from three resource categories: vertebrate, invertebrate, or plant (for details, see [46]). Although diets vary across time and space [48], the available species-specific diet information is sufficient for macroecological analyses [46].

2.2. Continental ensemble species pools

We used two geographic ranges for mammals from Phylacine: current and present-natural (Fig. S1), both provided as rasters in Behrmann equal-area projection with raster cell resolution of 9000 km^2, 1^o wide. The current ranges included rasterized native ranges from the IUCN Red List Version 2016-3 [49]. The present-natural ranges, created by Faurby & Svenning [45], included counterfactual estimates of current, expected ranges for all mammals that have existed during the past 130 000 years, assuming late Quaternary range reductions had not occurred (for methods see [45]). To create present-natural ranges, all mammals were systematically reviewed for range reductions, except for non-threatened, small-bodied species (< 1kg), assuming these species were not impacted by humans. In total, 51% of species included in our analyses were systematically reviewed. To assess potential bias in our results because of the uneven review of species' range changes, all analyses were performed for all species, and only for species that were systematically reviewed.

Species range rasters were clipped, using 'mask' from the 'raster' package [50] using R Version 3.5.1 [51] to an estimated Late Pleistocene land map (Fig. S3) to remove species ranges from islands not connected to continental mainland by land bridges during the last glacial maximum.

To measure a species' continental range size, we masked its geographic range raster to a Behrman equal-area projected continental shapefile and summed the number of cells that fell entirely within a continent's border [52]. For each species, geographic range difference was calculated as the number of raster cells occupied in the current minus the present-natural ranges (Fig. S4). Out of 1081 species, 14% had smaller ranges in the current compared to the present-natural. As our focus was on range loss, four species with larger ranges in the current (coyotes, North African white-toothed shrew, least weasel and lesser white-toothed shrew) were classified as having unchanged geographic range.

2.3. Functional diversity of continental ensembles

We calculated functional diversity metrics from functional spaces for each continent and for current and present-natural ranges separately, using the 'FD' package [53]. We scaled and centred traits of $\log_{10}$-transformed body mass and the three dietary traits by subtracting the means and dividing by the standard deviation. To calculate continental functional spaces, we calculated a dissimilarity matrix for all species using Gower's distance because of unequal weighting of traits (body mass: 1, each dietary trait: 1/3). Principal coordinate analysis (PCoA) was performed on the dissimilarity matrix, using the 'dbFD' function which returns PCoA axes to construct functional spaces. We incorporated the first four PCoA axes into our analyses, as recommended by Maire *et al.* [54], which captured 73% of trait variation. The variance explained by each axis was calculated by the sum of eigenvector values, divided by the value of each axis. Each PCoA axis was explained by a combination of the original functional traits (Fig. S5). A global functional trait space was calculated using all species (Fig. S6), with continental functional spaces extracted as subsets of species present in a continental ensemble.

We calculated two functional diversity metrics, functional richness (FRic) [55] and functional dispersion (FDis) [56] for the current and present-natural ensembles for each continent. FRic was calculated as the minimum convex polygon for each continental functional space relative to the global 4-D functional space, scaled from 0 (no functional space) to 1 (global functional space). FRic is unaffected by range size weighting. FDis involves calculating the functional space centroid, which can be weighted by a given metric (i.e. abundance). Here, FDis was calculated first as the average distance of species from the centroid of the species functional space without weighting (i.e. presence/absence) (Fig. S5), and second with weighting by each species' continental geographic range, which shifts centroids towards species with larger ranges (Fig. S7). Lower values of FDis indicate higher species similarity, whereas higher values indicate higher species dissimilarity within an ensemble.

2.4. Statistical analyses

2.4.1 Identifying traits influencing differences between current and present-natural geographic ranges

To investigate factors influencing differences between current and present-natural ranges of carnivorous mammals, we fitted binomial Bayesian phylogenetic mixed models (BBPMMs) accounting species' shared ancestry [57] using the 'MCMCglmm' package [58]. We used phylogenetic trees from the Phylacine database and took average estimates (log-odds ratios) and upper and lower 95% credible intervals from 100 sampled phylogenetic trees and BBPMM models using the 'mulTree' package [59], to account for phylogenetic uncertainty. The response variable was the proportional range reduction expressed as the number of lost and currently occupied raster cells. We included all species in our models with extinct species (n = 26 species) coded as having a 100% range reduction. Scaled and centred predictor variables included body mass ($\log_{10}$(g)) and vertebrate consumption (%).

Each model was run for 200 000 iterations, with burn-in period of 10 000 and thinning interval of 100. We checked model chain convergence using the Gelman-Rubin statistic, the potential scale reduction factor (PSR), with all models having a PSR < 1.1 [60]. As recommended by Hadfield [61], and as used by Healy et al. [62], we used an uninformative inverse-Wishart prior distribution (variance, $V = 0.5$, and belief parameter, $nu = 1$). As in Healy et al. [62], we used a hierarchical partitioning method for model selection by running models with each variable individually and with interactions, to identify trait combinations best explaining proportional range reduction. The model structure with the lowest average deviance information criteria (DIC) value was selected as the best-supported model [63].

2.4.2 Continental ensemble functional diversity and functional space structural change

To test for differences in FDis and FRic between current and present-natural ensembles, we performed non-parametric Wilcoxon signed-rank tests, using each continent as an independent observation. Differences in continental functional space between current and present-natural were investigated by assessing magnitude and directional shift of the ensemble centroids. To assess directional difference in functional space, we calculated centroid shifts along each of the four principal coordinate axes from the current to present-natural for each continent. We used Kruskal-Wallis tests to test for differences in the magnitude of centroid shifts between axes for both weighting methods separately. Post-hoc Dunn-tests identified pairwise differences. Mann-Whitney tests were used to investigate differences in magnitude of centroid shifts within each

of the four functional space axes when calculating FDis as unweighted (presence-absence) and weighted (geographic range size).

3. Results

3.1. Traits influencing differences between current and present-natural geographic ranges

After controlling for phylogenetic relatedness, the best supported model for predicting species geographic range differences (Table S1) included an interaction between body mass and vertebrate consumption (Table S2). Increases in body mass resulted in greater geographic range differences (BBPMM; body mass: log-odds ratio estimate [E] = 9.11, credible intervals [CI]: 6.58-11.97), the effect of which increased with higher vertebrate consumption (Fig. 1; interaction term: E = 1.52, CI: 0.13-2.97). In re-analyses including only systematically reviewed species, the best supported model was the same (Table S3), although the significant interaction between body mass and diet was lost, with body mass being the only significant predictor (Table S4; Fig. S8).

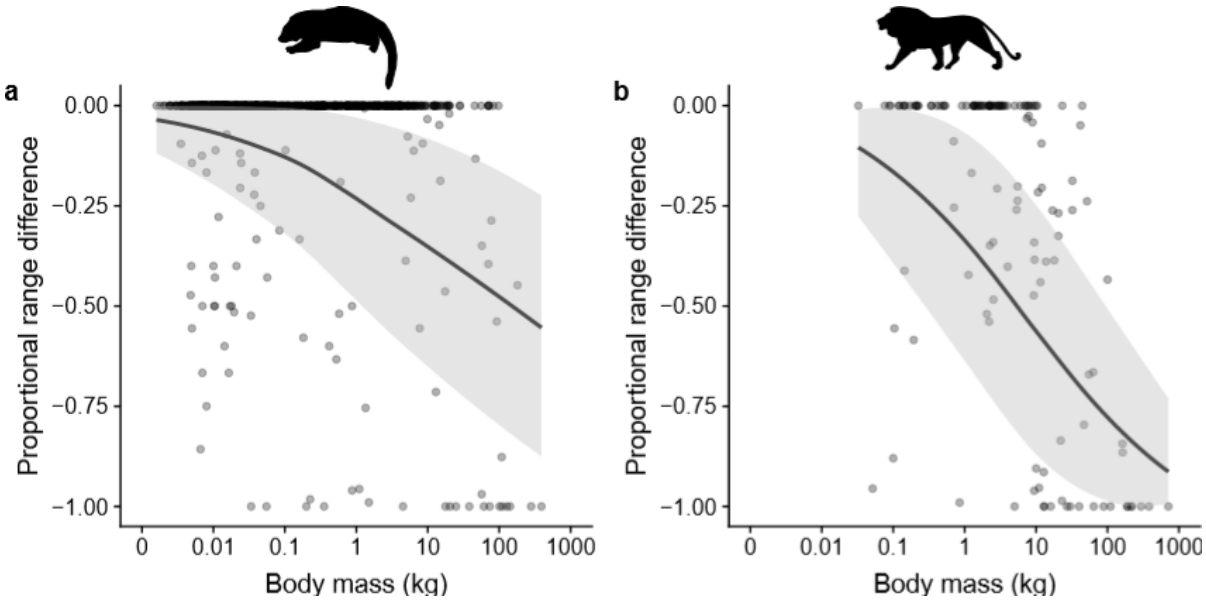
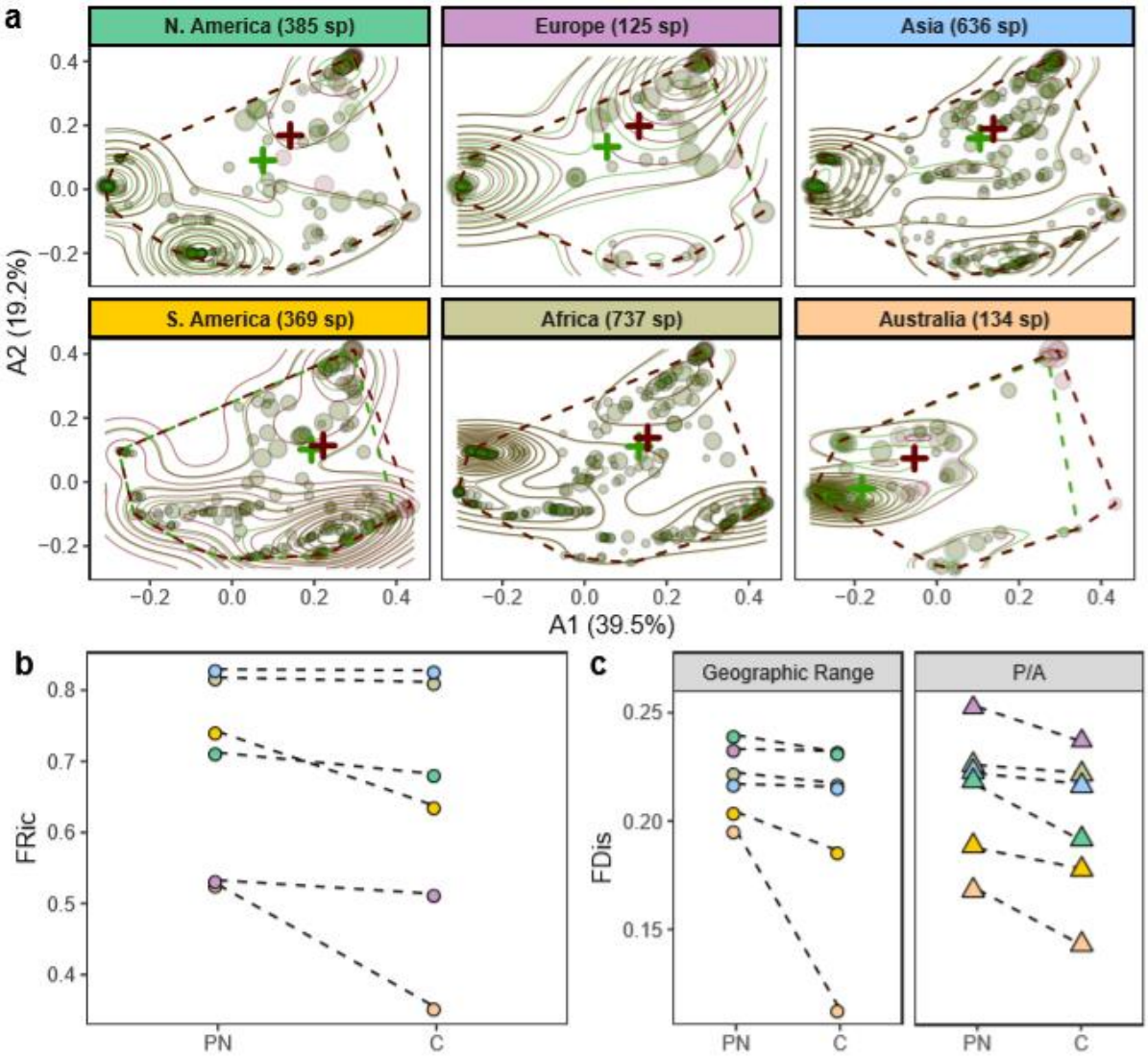


Figure 1. Proportional difference between current and present-natural species' geographic ranges (points with equal transparency) increased with greater body masses (log_{10}(kg) for interpretability). The effect was greater for species with increased vertebrate meat consumption, shown for illustration for (a) non-hypercarnivores (5-69% vertebrate meat, e.g. binturong), and (b) hypercarnivores (≥70% vertebrate meat, e.g. African lion). Average BBPMM estimate (black line), accounting for shared ancestry, is shown with upper and lower 95% credible intervals (shaded area).

3.2. Continental ensemble structural shifts for carnivorous mammals

All continents experienced similar structural shifts in functional diversity when comparing current to present-natural ensembles when weighted (Fig. 2a) by geographic range and unweighted (Fig. S9). Current FRic was lower across continents, indicating loss of species with the most extreme traits (median relative decline: -3.9%, lower quartile (Q2): -1.5%, upper quartile (Q4): 11.7%; Wilcoxon signed-rank test, $W= 21$, $p < 0.05$; Fig. 2b). The relative magnitude of FRic difference varied from 32.9% for Australia to 0.1% for Asia. Current FDis was consistently lower across continents, indicating increased similarity in species functional traits; FDis was lower both weighted by geographic range (-2.8%, Q2: 7.5%, Q4: 1.1%; $W = 21$, $p < 0.05$; Fig. 2c) and unweighted (-5.6%, Q2: 10.3%, Q4: 2.9%; $W = 21$, $p < 0.05$; Fig. 2c). The largest relative difference in FDis when weighted by geographic range occurred in Australia (42.2%). However, on average, we detected a near two-fold relative increase in FDis decline between the current and present-natural for the unweighted compared to weighted analysis. The reason for this was that the FDis-weighted centroids in the present-natural occurred in a species-rich location of trait space (causing a lower average distance from species) and shifted towards less species-rich locations. Alternatively, unweighted centroids began in less species-rich locations (a higher average distance from species) and shifted to more species-rich locations of trait space, causing a greater negative difference in the FDis metric for the current ensemble. Analysis with systematically reviewed species showed similar trends (supplementary results), except for FDis difference in Europe, which increased when using unweighted FDis (Fig. S10), likely because almost all small insectivores were not systematically reviewed.



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239 **Figure 2.** Functional diversity differences between present-natural and current ensembles for
240 each continent. (a) Continental functional trait spaces (species richness in parentheses) shown
241 using the first two PCoA axes with species represented by points (size scaled to geographic
242 range size) for present-natural (PN; brown) and current (C; green) ensembles. For simplicity,
243 only the first two axes of change in functional richness are shown here by minimum convex
244 polygons (dashed lines) for PN and C ensembles for each continent, explaining 59% of the
245 variance, despite it being calculated from the first four axes. Functional dispersion is
246 represented by the distance of all species from the ensemble centroids (crosses) representing
247 the weighted centres of the functional hypervolumes, with the weight being species' geographic
248 range size. (b) Differences in the 4-dimensional functional richness (FRic) for each continent
249 between the PN and C ensembles. (c) Difference in functional dispersion (FDis) between
250 current and present-natural ensembles for each continent, calculated using two weighting

methods: geographic range-weighted (left, circles) and presence-absence (P/A) only (right, triangles). Colours in b & c represent continents, colours as in a.

Comparing between present-natural and the current, continental ensemble centroids displayed similar directional shifts along axes in functional space (Fig. 2a & Fig. 3). The centroid shift magnitude was significantly different between the four functional trait axes for unweighted (Kruskal-Wallis: $\chi^2 = 18.75$, df = 3, $p < 0.001$) and weighted analyses ($\chi^2 = 17.62$, df = 3, $p < 0.001$). Continental ensembles shifted towards smaller-bodied and more insectivorous species, and away from hypercarnivorous species towards more herbivorous species, as indicated by shifts on A1 and A2, respectively.

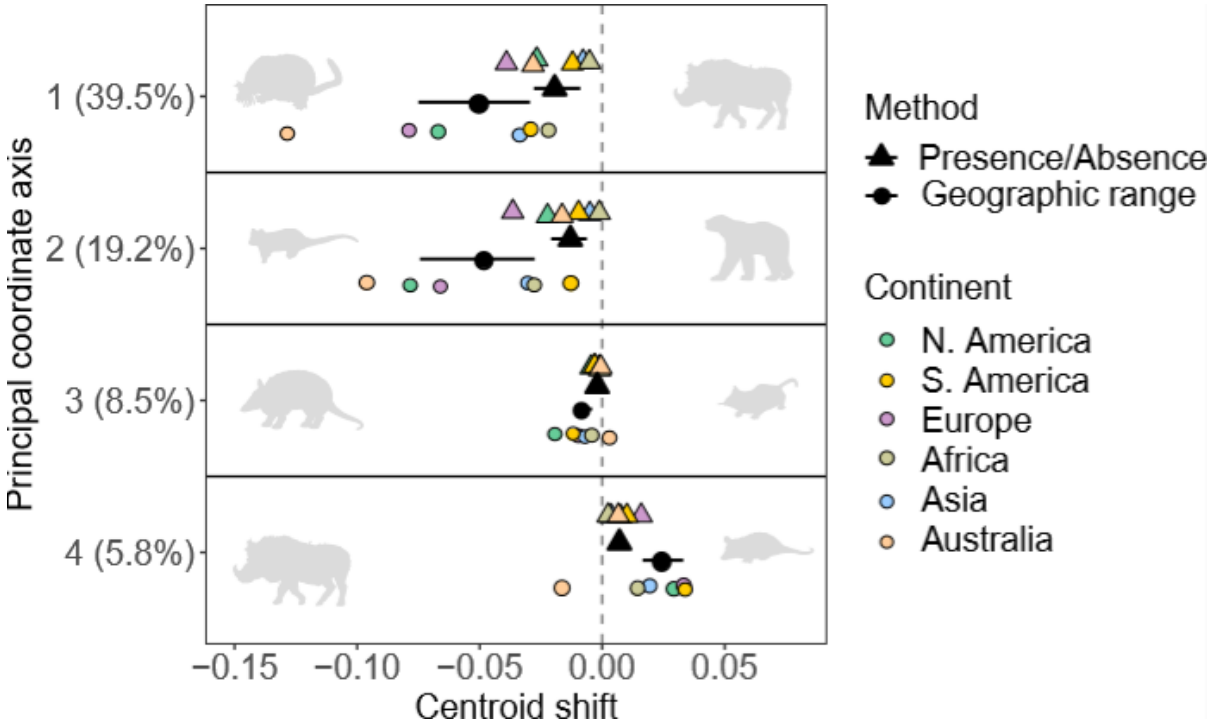

Figure 3. The magnitude of continental ensemble centroid shifts between present-natural and current ensembles for each continent (coloured points) along the four PCoA axes of functional space (73% total variance). We used two different weighting methods: with geographic range (circles) and presence-absence only (triangles). Axis medians and interquartile ranges shown by black symbols and lines, respectively. Silhouettes highlight species at the extremes of functional space, including from high to low values: *Metridiochoerus compactus*† (extinct) to Alaska tiny shrew (A1), *Arctodus simus* (extinct) to long-tailed pygmy possum (A2), giant armadillo to montane African climbing mouse (A3), and gray four-eyed opossum to *Metridiochoerus compactus* (extinct) (A4). Negative shifts along A1 indicate shifts towards smaller species with more insectivorous diets. Negative shifts on A2 indicate shifts away from

more carnivorous to more herbivorous species. Positive shifts along A3 indicate shifts away from larger-bodied insectivorous species. Positive shifts along A4 indicate shifts away from large-bodied dietary specialists towards medium-bodied dietary generalists.

We detected a significant difference between the two weighting methods in the magnitude of the centroid shift along A1 (Mann-Whitney: $U = 5$, $p < 0.05$), and A2 ($U = 5$, $p < 0.05$), with geographic range weighting causing a 2.5-fold greater shift than using presence-absence only on A1, and 3.6-fold greater shift on A2. For systematically reviewed species there were, generally, shifts away from hypercarnivorous to more herbivorous species (A2). The exception was South America where ensembles shifted slightly towards hypercarnivores when using geographic range size as a weighting (Supplementary results; Fig. S11). A shift from larger-bodied to smaller-bodied species (A1) is still detected, although no significant difference between weighting methods. Similar results were seen on A3 and A4 compared to the full dataset, with geographic range weighted centroid shifts being greater on A3.

4. Discussion

The global geographic ranges of carnivorous mammals are currently more reduced for species with greater body mass and with higher specialisation on vertebrate meat, as a result of late Quaternary extinctions and range contractions. This bias towards large-bodied, hypercarnivorous clades following ecological disturbance has been a common occurrence throughout mammalian evolution [64,65]. Trophic specialisation on large prey and intrinsic traits, such as low population densities, likely increases vulnerability of large-bodied hypercarnivores to ecological disturbances, such as the arrival of competitors [64,65]. This is analogous to the effects of modern humans which have competed with carnivores through prey exploitation [66], habitat modification [67], and direct persecution [68]. The loss of megafauna around the world [15] has reduced the diversity of resources for both predators and scavengers [32,69,70]. The selection against large, hypercarnivorous mammals is consistent with human-induced niche filtering [41,71], resulting in functional homogenization of carnivore ensembles globally [38]. Despite diet varying potentially across space [72] and time [79] for some taxa, our study revealed continental ensembles have become increasingly ecologically similar as smaller-bodied, less carnivorous mammals have been more resilient to disturbances in the late Quaternary, a phenomenon predicted to continue into the future in response to anthropogenic pressures [1].

Despite range reductions of large-bodied, hypercarnivorous mammals having occurred across all continents, the magnitude of change varied. Australia suffered the largest relative decline in its carnivorous mammal ensemble, primarily because of the originally low functional redundancy of the continent's hypercarnivorous mammals. This was previously unreported because of taxonomic focus of research on Carnivora [27]. Furthermore, the loss of functional diversity for mainland Australia is likely underestimated because the only extant, native hypercarnivorous (100% vertebrate meat) mammal, the Tasmanian devil, is restricted to Tasmania. The native, highly-carnivorous tiger quoll, which still occurs on the mainland, also consumes a relatively high (30%) proportion of invertebrates. However, the dingo, an apex predator potentially introduced by humans, likely buffers the loss of functional diversity for the Australian ensemble [74]. In North America and Europe, ensembles have also suffered large structural shifts away from large-bodied and hypercarnivorous mammals, which was reflected in loss of functional richness and consistent with previous research [75]. This may, in part, be explained by generally more research on these continents [76] and greater knowledge of species' range contractions. The South American ensemble experienced a large decline in functional richness, influenced by the loss of large-bodied, and primarily herbivorous, short-faced bears *Arctotherium tarijense* and *A. wingei*. The functional diversity and ensemble structure of carnivorous mammals in Asia and Africa have been less affected by late Quaternary extinctions. The large shift away from large-bodied hypercarnivorous species on continents would likely be even greater with wider taxonomic inclusion. In Australia, large-bodied, hypercarnivorous reptiles, including a large snake (*Wonambi naracoortensis)*, monitor lizard (*Megalania prisca)*, and terrestrial crocodile (*Quinkana sp.*), went extinct shortly after the arrival of modern humans [77]. Including large scavenging birds whose range reduction was caused by the decline in megafauna carcasses in the landscape [73], would further influence shifts in carnivorous species' functional diversity.

Geographic range contractions have been observed for a variety of taxa across the world [78], with many extant carnivorous mammals having suffered large range contractions [13,28]. Our findings demonstrate that only considering extinction events, and not including geographic range size, likely leads to underestimates of ensemble structural changes at large spatial scales, although not necessarily changes in functional diversity metrics. This was particularly evident in the functional space axes relating to body mass and vertebrate consumption, which both had a roughly three-fold greater shift in the ensemble centroid position when weighted by geographic range compared to presence-absence alone. Shifts of this magnitude were expected

for body mass because of the correlation between range size and body mass [79]; however hypercarnivory, alongside large body mass, was also another previously widespread functional trait that is now severely geographically restricted across continents. This may, in part, be influenced by the known, current range of large-bodied, hypercarnivorous species being smaller as they tend to have been studied in more depth [80], resulting in increased fragmentation and range loss (Supplementary methods, Table S5, and Fig. S12-13). However, such species are likely to have comparatively highly fragmented ranges in reality in response to anthropogenic pressures [30,81]. Although the lack of range reduction for small-bodied species is influenced by many not being systematically reviewed, this likely reflects reality because of the well described bias towards large body size extinctions during the Late Quaternary [15].

The shift of ensembles away from hypercarnivorous species across continents likely has global consequences for ecological processes. Predatory hypercarnivorous mammals have the potential to exert top-down forcing on prey populations both directly and indirectly [74,82–85], and influence the distribution of nutrients in ecosystems [86]. Removal of predators can lead to increased herbivore densities [87] and cause mesopredator release [26]. In Australia, removal of top-down forcing by apex predators has resulted in introduced mesopredators becoming abundant [88], while the presence of apex predators has been shown to benefit native biodiversity [89]. Reintroducing, or facilitating natural recolonization, of large predators may counteract these effects, with top-down effects demonstrated through herbivore behavioural changes in response to grey wolves in Yellowstone National Park [90] and Europe [91], the effects of predator auditory and scent cues on bushbuck in Mozambique [25], and the influence of dingoes on mesopredator populations in Australia [92]. In Australia, reintroduction of the hypercarnivorous Tasmanian devil to the mainland could (re-)introduce top-down forcing on non-native mesopredators [93],although, dingos are argued to already exert greater top-down pressures on mesopredators [94] and capable of restoring the large predator guild [95]. While these are active processes, restoring predator guilds could be achieved passively by promoting natural recolonization of predators, as seen in Europe [96], and incorporating management decisions to minimise human-carnivore conflict [97]. Although the range expansions of four species were excluded here, future research could assess the effects of such range changes, and include introduced species, to understand the full spectrum of continental ensemble functional change related to human-impacts.

The interacting effects of humans and changing climates throughout the late Quaternary have resulted in reductions in the current global ranges of large-bodied, hypercarnivorous mammals, compared to a counterfactual scenario in which humans had not migrated out of Africa. Range reductions have resulted in globally consistent structural shifts in continental carnivorous mammal ensembles, with the greatest loss of native functional diversity having occurred in Australia. While functional homogenization of carnivorous mammals will likely continue to occur in the coming century [1], we show that this process is already underway as continental ensembles have shifted towards smaller-bodied, less carnivorous species. We recommend enhanced protection of large-bodied, hypercarnivorous mammals, as well as identifying regions for reintroductions, facilitating natural recolonizations, and accepting already introduced apex predators, to reverse past attritions and preserve trophic complexity of current and future ecosystems.

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7. Contributions

OSM collated data, performed analyses and wrote the first manuscript draft. OSM, CJS and JPWS contributed to the conception and development of analyses, interpretation of data, and manuscript revision.

8. Data accessibility

All analyses were performed using data from the PHYLACINE database accessed through Github (Version 1.2; *https://github.com/MegaPast2Future/PHYLACINE_1.2*).

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